BIOGEOGRAPHIC VARIATION IN THE BABOON:

DISSECTING THE CLINE

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SUMMARY

All species demonstrate intraspecific anatomical variation. While generalisations such as Bergman's and Allen's rules have attempted to explain the geographic structuring of variation with some success, recent work has demonstrated limited support for these in certain Old World monkeys. This study extends this research to the baboon: a species that is widely distributed across sub-Saharan Africa and exhibits clinal variation across an environmentally disparate range. This study uses trend surface analysis to map the pattern of skull variation in size and shape in order the visualise the main axes of morphological variation. Patterns of shape and size controlled shape are compared to highlight morphological variation that is underpinned by allometry alone. Partial regression is used to dissociate the effects of environmental terms, such as rainfall, temperature, and spatial position. The diminutive Kinda baboon is outlying in size so analyses were carried out with and without this taxon.

Skull size variation demonstrates an east-west pattern, with small animals at the two extremes and large animals in central and southern Africa. Shape variation demonstrates the same geographical pattern as skull size, with small sized animals exhibiting classic paedomorphic morphology. However an additional north-south axis of variation emerges. After controlling for skull size, the diminutive Kinda baboon is no longer an outlier for size and shape. Also the east-west component is no longer evident and discriminant function analysis shows an increased misclassification of adjacent taxa previously differentiated by size. This demonstrates the east-west component of shape variation is underpinned by skull size, while the north-south axis is not. The latter axis is explicable in phylogenetic terms: baboons arose in southern Africa and colonised East and West Africa to the north, diverging in the process, aided by climate-mediated isolating mechanisms. Environmental terms appear poorly correlated with shape variation compared with geography. This might indicate that there is no simple environment-morphology association, but certainly demonstrates that phylogenetic history is an overbearing factor in baboon morphological variation.

KEYWORDS

Clines, subspecific variation, baboon, *Papio hamadryas*, environment, morphological variation.

INTRODUCTION

Continuous and spatially structured anatomical variation makes up a large part of intraspecific diversity (Forsman and Shine, 1997, Thorpe, 1987). Clinal variation in size is common (Millien et al., 2006, Mayr, 1956, Ashton et al., 2000), with patterns often being similar between species (Bergmann, 1847, James, 1970, Millien et al., 2006). The most well-known examples of this are

Bergmann's 'rule' and Allen's 'rule.' These ecogeographic principles describe how body and extremity size covary with temperature in closely related animals, with spatial descriptors such as latitude or altitude often being used as proxies (Mayr 1963, Bergmann, 1847; Allen, 1877). Meta-analyses, suggest that over 70% of mammals and birds conform to Bergmann's rule of increasing size with distance from the equator (Millien et al., 2006). In addition species as disparate as non-migratory sea birds (Nudds and Oswald, 2007), jackrabbits (Griffing, 1974) and foxes (Millien et al., 2006) exhibit intraspecific variation consistent with Allen's rule of decreasing extremity length with distance from the equator. However, temperature is not the only spatially-correlated potential influence on morphological variation. Greater primary productivity is likely to equate to greater food availability, a known influence on animal size and thus a possible determinant of clinal variation (Ferguson and Larivière, 2008, Yom-Tov and Geffen, 2006). Seasonality may also affect body size (Boyce, 1978). Seasonal reductions in the amount of sunlight results in reduced photosynthesis, compounding the deleterious effects of low temperature and low rainfall. For diurnal animals there is also the added burden of reduced foraging time during part of the year (Hill et al., 2003). One strategy for coping with seasonal fluctuations of food is to accumulate fat over the summer months and use this to make up the negative energy balance over the winter (Lindstedt and Boyce, 1985). As stores are proportional to absolute size, some researchers have claimed that increasing size with latitude is selected for to act as a buffer to seasonal food shortages (Millar and Hickling, 1990, Boyce, 1978, Lindstedt and Boyce, 1985), for which there is evidence in carnivores (Ferguson and Larivière, 2008). The likely importance of resource availability led Reinig (1939, reported in Scholander, 1955) to refute the existence of Bergmannian clines altogether, stating that size clines were present from the core to the periphery of an animal's range. This, he argued, was because peripheral habitat at the environmental boundary of an animal's range may represent sub-prime habitat.

Despite a wealth of studies in other orders, clinal variation in primates and its environmental underpinnings is relatively unstudied, with existing research providing few generalities. For instance the long-tailed macaque exhibits a limited Bergmannian size cline but the pig-tailed macaque does not (Schillaci, 2009). An east-west rather than Bergmannian trend was found in Geoffroy's tamarin (Natori and Kondo, 1998) and Brazilian tufted-eared marmosets (Albrecht, 1982). In several studies the pattern of clinal variation is mosaic rather than affecting the whole body equally, such as in Japanese macaque maxillary sinus volume (Rae et al., 2003) and vervet tail length (Turner et al., 1997). Instances of translocation show that environment does influence body size. Macaques translocated from Japan to two locations in the USA exhibited larger size at the colder Oregon site than those at the warmer Texas site, corresponding to a decrease in surface area to body mass of

about 10% (Paterson, 1996). The time depth was only two generations, suggesting phenotypic plasticity (Paterson, 1996). A more consistent and comparable set of studies reveal strong clinal variation in three widespread African primates. Blue monkeys (Cardini et al., 2010), vervets (Cardini et al., 2007) and red colobus monkeys (Cardini and Elton, 2009) have all been found to exhibit a decreasing size cline from Central to East Africa. However, there are differences, as West African blue monkeys and red colobus are small while West African vervets are large (Cardini et al., 2007, Cardini et al., 2010, Cardini and Elton, 2009, Cardini et al., 2012). The Central-East African trend was found to be correlated with average annual rainfall in vervets, arguing for a resource-based underpinning (Cardini et al., 2007).

It is possible that the similarities in size trends are the result of a common response to environmental variation. One way of further addressing this is by extending analyses to other species. The baboon, with its spatially structured variation and extensive geographic distribution (Fig. 1), is an excellent candidate for this, through mapping and quantifying the correlates of its variation. An Old World monkey, like the vervet, red colobus and blue monkey, this species is found almost continuously in sub-Saharan Africa, aside from true desert and rainforest (Fig. 1, Jolly, 1993, Alberts and Altmann, 2006). Since the baboon is terrestrial, it provides good comparison for the two arboreal primates (blue monkeys and red colobus) and one terrestrial primate (vervet) studied in this fashion to date. The baboon is regionally variable in pelage and morphology, and variants are often grouped into subspecies (Jolly, 1993). While forms may be regarded as discrete, there is no complete reproductive isolation between them, with hybridisation common at the borders and evidence of a long history of genetic introgression (Zinner et al., 2011, Zinner et al., 2009). Animals next to the hybrid zone exhibit some of the traits of those on the opposite side, unlike those closer to the heart of the subspecific range (Jolly, 1993). Thus, the baboon may be approximately modelled as a continuous cline (Frost et al., 2003). Such an approach revealed that geographic position explained 60% of 'size-sex-corrected' cranial shape variation (Frost et al., 2003). Across Africa, Frost et al. (2003) found evidence of morphological change in a northeast-southwest direction, with the greatest step between northern and southern taxa. Northern forms had wider skulls and less ventrally flexed rostra than southern forms. However, the absence of analyses on size differences and the size correction used by Frost et al. (2003) renders comparison with other monkeys difficult, as size is a major part of subtle clinal morphological variation, and is likely to be the most important ecological aspect (Peters, 1983).

Baboon size variation is extensive, with the chacma baboons (*P. h. ursinus*) in southern Africa having a large body size (Anderson, 1982) while hamadryas (*P. h. hamadryas*) and Guinea baboons (*P. h. papio*) being smaller (Jolly and Phillips-Conroy, 2003, Jolly and Phillips-Conroy, 2006). Baboon size and shape is undoubtedly spatially variable but it is not clear whether this variation has arisen in response to environmental pressures, as has been argued to be the case in other instances of clinal variation (James, 1970, Burnett, 1983, Ferguson and Larivière, 2008, Virgós et al., 2011). This seems likely in baboons as they are extremely responsive to the environment, which modulates group size (Byrne et al., 1993, Kunz and Linsenmair, 2008), composition (Hamilton III and Bulger, 1992, Kunz and Linsenmair, 2008) and hierarchy (Barton et al., 1996) and alters time budgets according to day length (Hill et al., 2003), rainfall (Bronikowski and Altmann, 1996) and temperature (Hill, 2006). However, although Dunbar (1990) found a relationship between rainfall and body mass, recent analysis with fuller data show this is not the case across the *Papio* baboons as a whole, although there is some evidence for a relationship within subspecies (Jolly, 2011). Evidently the relationship between environment and morphology is complex and requires additional research to elucidate further.

The aims of this study are to establish the patterns of baboon size and shape variation, and quantify the magnitudes of environmental and spatial variation that underpin this variation. Size is considered more responsive to the environment than shape (Marroig and Cheverud, 2005). Size-related (allometric) and size unrelated components of shape thus reveal different processes, with deviations from allometric scaling suggesting deeper phylogenetic differences (Marroig and Cheverud, 2005). In contrast, morphologies differing chiefly in allometric scaling are more likely to be the product of different ecological forces (Marroig and Cheverud, 2005), mediated by life history tradeoffs in growth and reproduction relating to resource abundance and predation pressure (Palkovacs, 2003, Whitten and Turner, 2009, van Schaik, 1992, Charnov, 1993). The intraspecific pattern and underpinnings of intraspecific variation will be compared with the ecologically analogous vervet, and the arboreal blue and red colobus monkeys. The presence of affinities might suggest convergent adaptation, while idiosyncrasies suggest unique responses or evolutionary trajectories. This will advance our understanding of the emergence of clinal variation in primates and mammals in general.

METHODS

Sample

Anatomical landmark data for museum skulls from 463 *Papio hamadryas* subspecies were taken from the Leverhulme Old World monkey database (Elton and Cardini, 2008). Each specimen was described by 86 three-dimensional craniofacial landmark coordinates (Table 2). This sample was reduced to include only well provenanced specimens (with latitude and longitude data or a place name for which they could be found), resulting in 370 specimens. Subspecies was designated on the basis of specimen location. The original dataset contained landmark data for only the left half of the skull, and in a minority of the specimens landmarks were missing. These issues were addressed using the method outlined fully in Cardini et al. (2010), which involves performing a GPA, estimating the coordinates of missing landmarks, and reflecting and reuniting the skull to create a complete conformation.

Summarizing Shape

The major axes of shape variance of the coordinate data are summarised by principal components (Slice, 2007). To calculate the optimal number of PCs to use (i.e. the fewest that describe most of the total variance), the correlations between the Euclidean distance matrix (ED), based on the PCs and the Procrustes distances matrix (PD) were examined for sequentially smaller numbers of PCs. The 'elbow' or 'drop-off point' in the relationship represents a good trade-off between accuracy and economy of PC inclusion, given that when all PCs are included the matrices correlate perfectly (Cardini et al., 2010). Variation in specimen morphology within groups was visualised, and outliers were identified using bivariate plots and UPGMA cluster analysis of the PCs. A few morphological outliers were assumed to be the result of measurement mistakes, or else pathological factors of no interest with respect to this study, and were excluded from the analysis, resulting in the study sample of 361 specimens (table 1).

Sex-Correction

Given the small female sample, female morphology was 'masculinised' (Cardini et al., 2010). This was achieved by adding within each subspecies the difference between male mean and female mean to female size (univariate) and shape (multivariate: differences per coordinate) values. This approach has the dual advantages of boosting the geographic sample and avoiding non-robust comparisons between the sexes.

Geographical Averaging

Specimen localities were not evenly distributed. Certain localities were represented by only a single skull while other localities yielded up to ten specimens. Such local clustering is likely to skew the

results of an overall trend as regressions minimise variance, and much of the variance is concentrated in a particular regions. By averaging the morphological data (the 86 landmark coordinates) for specimens in the same locality the variance is more evenly weighted. 50km buffers around each locality were calculated in ArcGIS (ESRI, 2009) and were used to work out which specimens should be averaged. Microsoft Excel (2007) was used to average landmark configurations using the average function. Different taxa were not averaged because of our *a priori* expectation of difference in morphology.

Spatial variation in morphology was investigated using trend surface analysis (Legendre and Legendre, 1998), a method that regresses variables onto longitude (x) and latitude (y). While there are more sophisticated methods, this method is simple, and easy to interpret and has been demonstrated for other African monkeys to provide results concordant with more complex analyses such as thin plate spline and kriging (Cardini et al., 2012, Kent personal communication). In this study, we regressed the first 20 PCs of shape (this number being derived according to the method described), and separately size, simultaneously onto a polynomial expansion of longitude (x) and latitude (y) (binomial: x2 xy y2, and trinomial: x y x^2 xy y^2 x^3 x^2y xy^2 y^3) and progressively removed the most non-significant predictors until only significant ones were left. To compare the fit of the models, the variances explained by each regression were calculated. Size was plotted directly on a map. Shape, characterised by PCs, is multivariate, and so cannot be plotted simply. In the case of shape, a PCA of the predicted PCs was carried out using NTSYSpc (Rohlf, 2008), resulting in geospatial PCs (gsPCs) (*sensu* Cardini and Elton, 2009). These PC scores were plotted on a map as contours to represent shape variation as a function of latitude and longitude, using ArcGIS (ESRI, 2009). To test the robustness of the geospatial PCs, the analysis was carried out on three reduced datasets, each comprising a random two thirds of the full dataset. This randomisation was achieved by numbering the specimens in threes and choosing two of the three numbers for each holdout. Subspecies were grouped, and so this procedure results in reduction that was equal across subspecies, and so no holdout had one subspecies overrepresented by chance. The degree of similarity between the patterns of the actual and reduced datasets indicates the relative robustness of the trend. Confidence in each holdout was measured by using this trend to account for the variance of the held out third, with higher values denoting better a better model.

High deviation from observed values adjacent to the Kinda baboon, and corresponding low variance of the full baboon trend surface analysis, as well weakly predicting holdouts, argued for the analysis

of the baboons without this outlier. Thus all analyses were carried out with and without the Kinda baboon.

Environmental Variable Selection

Raw environmental point data for every 0.5 decimal degree coordinates for precipitation, moisture index, and temperature were taken from the Wilmott & Matsuura database (Willmott et al., 1998, Willmott et al., 2001, Willmott and Matsuura, 2001). Rasters, surfaces with values for all pixels, were extrapolated from these point data using the variance minimising *interpolate* function in ARCGIS (ESRI, 2009). Normalised difference vegetation index (NDVI) for Africa (Zinner et al., 2001, Willems et al., 2009, Townshend and Justice, 1986), a remotely detected measure of photosynthetic activity, was downloaded from the Africa Data Dissemination Service (ADDS, 2005). Altitude was derived from the Earth Resource and Information Center (USGS, EROS). The ArcGIS Spatial Analyst and Extract to Points function were used to obtain values from all environmental rasters for each specimen according to its latitude and longitude. Monthly means, standard deviations and ranges were calculated for precipitation, moisture index, temperature and NDVI. Other indices found to be informative in previous studies of primates, P2T (the number of months where precipitation (mm) is twice the temperature ($^{\circ}C$)), seasonality index and Shannon Rainfall index (Bronikowski and Webb, 1996, Korstjens and Dunbar, 2007), were also calculated. These values were used in a partial regression (Legendre and Legendre, 1998). Because partial regression simply separates variation between two blocks, in this case environment and spatial variation, it is rather hard to work out what variables within that block are important. To get an insight into the environmental block, and also establish if there were disparate trends between taxa, centroid size was also regressed onto NDVI, altitude, mean and standard deviation of temperature, mean and standard deviation of precipitation, moisture index and Shannon diversity index.

Partitioning Spatial and Environmental Terms

Partial regression (Legendre and Legendre, 1998) was used to partition the morphological variation correlated with environmental variables (the environment block) from that correlated with spatial variation (the spatial block). Practically, this procedure involved regressing size and shape onto both the spatial block (geographic coordinates from the TSA) and environmental block, as well as size and shape onto the two blocks separately. The first spatial-environmental regression yields the variance explained by both blocks, while the separate regressions contain the exclusive and overlapping proportions for each block. The exclusive components of spatial and environmental variation can

then be calculated by simple subtraction and algebraic substitution (see Legendre and Legendre, 1998).

Size Correction

Actual baboon centroid sizes for the specimens were plotted and variation modelled using trend surface analysis and the holdout procedure. Given the considerable size variation in the baboon subspecies (Fig. 2), with the Kinda baboon in particular being much smaller than the others, the trend surface analysis was performed including and excluding Kinda. Removal of the size-dependent component of shape was achieved by regressing shape onto size using a multivariate analysis of covariance model (Klingenberg, 2011). Using a taxon code as a covariate, the subspecies were tested for differences in intercept and slope. According to the result of this test (i.e., non-significant differences in slope) each subspecies was modelled as having different intercepts but identical gradients (Elton et al., 2010). Subspecies means were created for the overall average size, according to the predictions of the taxon-specific regression models, and size-free residuals (saved in SPSS Inc., 2009) were added to these subspecific shapes, resulting in 'size-corrected' shapes.

Subspecific Differences

Discriminant function analysis was used to assess the degree of similarity of subspecies (Elton et al., 2010). The ratio of misclassified and correctly classified individuals, after cross-validation, gives a measure of similarity (Cardini and Elton, 2011). For instance if two groups are always correctly classified they are clearly different, but if two samples have the same size and they are misclassified into the other group 50% of the time, there is no appreciable difference (Kovarovic et al., 2011 and references therein). DFA was used before and after the size-correction to establish the importance of size in subspecies distinctiveness.

RESULTS

Size

In order to display the pattern of size variation a trend surface analysis was performed, with values of skull centroid size plotted as contours on a map. The sharp size difference between the Kinda baboon and the other subspecies necessitates analysis both with and without this subspecies. The non-Kinda trend surface analysis (TSA) reveals a strong east-west cline of increasing then decreasing skull centroid size (Fig. 3 a), with the trend explaining 55.9% of the size variance. This pattern is borne out in the holdouts (Fig. 3, b, c, d). The TSA shows a north-south cline slightly less pronounced than the east-west one, with a peak around central Africa, rising again in South Africa. This trend is

weaker in two of the holdouts (Fig. 3b, 3c) and not present in one (Fig. 3d). When the Kinda baboon is included, the TSA has a much lower explanatory power, at 24.7% (Fig. 4a). The clinal pattern of increasing and then decreasing size from east to west is still present (Fig. 4a) and the with- and without -*P. h. kindae* TSAs are mainly different within and adjacent to the Kinda range. The three holdouts corroborate this (Fig. 4b, c, d).

Shape

In order to display the pattern of shape variation a trend surface analysis was performed, with values of geospatial principle components plotted as contours on a map. The first geospatial PC of baboon shape with *P. h. kindae* removed shows a depression in West and East Africa denoting low gsPC values, with central Africa at intermediate values, and southern Africa at high values (Fig. 5a). Low gsPC values correspond to a morphology exhibiting a short rostrum and mandible, large neurocranium and wide face compared to those with high gsPC values. In addition, low values correspond to less ventrally deflected rostrum, and the anterior part of the neurocranium is elevated relative to the occiput. The second gsPC (Fig. 5b) has a similar spatial pattern to gsPC1 with peaks located in West and East Africa, but a depression in Central Africa and a rise and drop in South Africa. The West and north-east morphology corresponds to a small face, large neurocranium and wide face relative to central Africa. The rostrum of the Central and southern form is concave while the larger is convex, in contrast to gsPC1. The third gsPC (Fig. 5c), which accounts for a smaller amount of variance, shows a peak along the coast of East Africa then decreases to the north and west. The eastern morphology exhibits a deep mandibular corpus in contrast to the west, as well as more flared zygomatic arches. The shape pattern (Fig. 5a) is similar to that of size (Fig. 3a) and indeed the first and second gsPCs, but not the third, are correlated with size (Table 3).

The gsPCs including the Kinda baboon (Fig. 6) shows affinities to the Kinda removed TSA (Fig. 5), differing chiefly in a depression slightly to the north of where the Kinda are found, as was the case with size (Fig. 4). Similar morphological extremes are detected to the Kinda-free TSA (Fig. 5).

Size-Controlled Shape

In order to remove shape variation related to the common allometric trajectory of baboon subspecies, size-related variation was regressed out. The resulting size-controlled data were subject to a TSA and plotted as contours as in other analyses. The first size-controlled gsPC reveals a north-south clinal trend (Fig. 7). The northern specimens have a shorter rostrum (i.e. increasing nostril - glabella distance) and a change from a concave to a convex rostrum, as well as a slightly shallower

mandible and a shorter, narrower head relative to the southern specimens. The second size controlled gsPC explains only a quarter of the variance explained by gsPC1. It displays an east-west trend with a maximum on the coast of East Africa, dropping off to the west and north. The third size-controlled gsPC indicates a complex clinal pattern. In West Africa the morphological differentiation is rather subtle, accounting 8.7% of the total variation, related mainly to the deeper mandible seen in West African specimens.

Subspecific Differences

To compare the similarity of the morphology of subspecies a cross-validated discriminant function analysis was carried out. *P. h. papio* and *P. h. kindae* are never misclassified (Table 4) while *P. h. hamadryas*, *P. h. ursinus* and *P. h. anubis* have some misclassification, with a trend toward misclassification into nearby groups for all but *P. h. anubis* (Table 4). Reclassification rates for the size-controlled sample (Table 4) show a slightly different pattern for all but *P. h. papio*. The majority of *P. h. hamadryas* specimens are misclassified as *P. h. anubis*. Two thirds of *P. h. kindae* specimens are misclassified as *P. h ursinus*, and over a quarter of the *P. h. ursinus* specimens are misclassified as *P. h. kindae*.

Environmental and Spatial Correlates

In order to establish the relative contribution of physical environmental terms and spatial positions to morphology partial regressions were carried out. In all partial regressions the spatial terms account for more variance than the environmental or shared ones (Table 5). Spatial terms account for a larger proportion of the variance in size when the Kinda baboon is removed (Table 5, Fig. 8). When Kinda is included, the partial regressions account for much less of the size variance (51.1% to 23.0%, Table 5). A slight increase in the environmental component is evident when the Kinda baboon is included (1.7% to 4.7%, Table 5). For shape, exclusion of the Kinda baboon makes little difference, with only a slight decrease in the dominant spatial component. There is little difference between the partial regression for full shape and the partial regression for allometrically controlled (Fig. 8). Regression of centroid size onto each of the separate environmental variables reveals no significant species-wide relationships and indeed only one significant relationship between centroid size of *P. h. anubis* and standard deviation of precipitation is evident (Table 6, Fig. 9).

DISCUSSION

This study has revealed marked variation in baboon skull size, shape and size-controlled shape. Skull centroid size is small in the western- and easternmost edges of Africa, and larger in central Africa.

This is contrary to Bergmannian expectations of size increasing north and south of the equator, suggesting that neither a straightforward thermoregulatory (Millien et al., 2006) nor seasonality buffering explanation (*sensu* Boyce 1978) can be invoked. Previous studies have indicated a close relationship between skull centroid size and overall body size (Singleton, 2002, Cardini et al., in press). The small bodied eastern- and westernmost subspecies, the hamadryas and Guinea baboons respectively, are on the furthest fringes of the baboon's current range. This may be consistent with the edge effect explanation (Reinig 1939, reported in Scholander, 1955). However, this hypothesis invokes decreasing habitat quality to account for small size. While the hamadryas baboon lives in a resource-poor environment (Schreier and Swedell, 2009, Kummer, 1968), the Guinea baboon lives in a very productive environment with high levels of rainfall, primary productivity and fruit abundance (Culot, 2003, Anderson and McGrew, 1984). There are several similarities between the far western and far eastern subspecies: small stature (Fleagle, 1988), pelage (Jolly, 1993), and social structure, namely a form of one male group (Maestripieri et al., 2007, Galat-Luong et al., 2006). It is thus parsimonious to regard these traits as ancestral, retained when baboons radiated into the north-eastern and -western corners of sub-Saharan Africa; the presence of the larger bodied olive baboon midway between the Guinea and hamadryas baboons may well be due to a later expansion of the ancestor of *P. h. anubis* (Jolly, 2003).

The lack of a Bergmannian trend is particularly surprising given that the chacma baboon from southern Africa is commonly regarded as the largest *Papio* subspecies (Fleagle, 1988, Anderson, 1982). Its large size is suggested to be an adaptation for heat conservation and starvation resistance (Anderson, 1982). Nevertheless, the central African baboons appear to occupy broadly the same contours as the chacma baboon in the size trend surface analysis. Larger size in forest baboons has been reported by Elliot (1909), who also identified slight differences in pelage and morphology. Rowell (1964, 1966) described an extensive suite of ecological and behavioural differences between forest baboons in Central Africa and savannah baboons in the East Africa. Resources at woodland sites are described as "superabundant" (Rowell, 1966), with baboons eating fruits, flowers, and barks. This habitat is seasonal but with consistent high quality food availability throughout the year. It is possible that forest baboons owe their large size to a release of the resource limitations faced by baboons on the savannah, a xeric and unproductive habitat, with a high seasonality of resource availability (Alberts and Altmann, 2006). During the dry seasons, foods in such environments can be poor quality and high fibre, such as roots, corms and tubers (Harding, 1976, Rhine et al., 1989, Norton et al., 1987).

Given the small skull centroid size of the West African Guinea baboon, food resource abundance does not satisfactorily explain size trends in all subspecies of *Papio hamadryas.* The partial regression analyses reveal that environmental terms explain only a small proportion of the total size and shape variance. As this block encapsulated primary productivity in the form of NDVI, this is at odds with a straightforward and consistent resource-based underpinning to clinal skull size variation in baboons. The regression of centroid size onto environmental variables revealed no consistent pattern across subspecies, or indeed any patterns within subspecies except for standard deviations of precipitation and centroid size in the olive baboon. Of course intraspecific analyses suffer from low sample size, in particular with Kinda and guinea baboons. Additionally the environmental variables may be somewhat removed from the factors that matter to the animals. For instance although NDVI, which gives a gross indication of the amount of photosynthesis (assumed to relate to the gross amount of food) is not a significant explanatory variable, resource distribution (varying between dispersed and clumped) rather than amount is known to affect group size via intragroup competition (Barton et al., 1996). Varying levels of resource availability per individual are likely to influence growth versus reproduction tradeoffs (Janson and van Schaik, 1993). Resource distribution and predation alter grouping behaviour in hamadryas baboons at Awash (Schreier and Swedell, 2012) and olive baboons at Laikipia and chacma baboons at the Drakensbergs (Barton et al., 1996). It is thus possible that the crude environmental variables fail to reflect such meaningful factors, such as resource distribution, and further studies incorporating socioecological variables will be required to investigate this.

The clinal pattern of shape variation largely mirrored that of size, with small animals exhibiting a classically paedomorphic appearance, with a relatively small face and relatively large neurocranium, as seen in vervets (Cardini et al., 2007) and red colobus monkeys (Cardini and Elton, 2009), as well as other mammals (Emerson and Bramble, 1993). However, the pattern of clinal shape change contained an additional north-south component of variation, in line with the findings of Frost et al. (2003). Removal of the size-dependent component of shape confirmed that the east-west trend is underpinned by size variation while the north-south cline is not. Comparison of the size-controlled and non-size-controlled DFAs also support this difference in pattern, highlighting important non-allometric shape differences within the species

The Kinda baboon is a notable outlier for size. While it grades into the larger yellow baboon to the east of its range (Freedman, 1963), this cline is sufficiently steep that it could not be well represented by a polynomial expansion in the trend surface analysis. Inclusion of this subspecies revealed an extensive trough in size and shape, placing adjacent large taxa at low size contours. This

deficiency of the model to deal with so steep a cline is demonstrated by the lower explanatory power of spatial terms in the partial regression with the inclusion of the Kinda baboon.

While the Kinda baboon was found to be an outlier in size, this was not so for size-controlled shape. This suggests that, though this animal has a distinctive paedomorphic morphology, it is distinct only insofar as it is allometrically scaled down relative to its neighbouring subspecies. Given the absence of any ecotone along the cline between the Kinda and the yellow baboon, there is no obvious environmental explanation for this small skull and body size. Behavioural observations hint at a possible social function. The Kinda baboon has reduced sexual dimorphism (Leigh, 2006, Jolly et al., 2011) with females exhibiting male-like vigilance and alarm behaviours, and males showing greater interest in nonoestrous females than exhibited by males of other subspecies (Phillips-Conroy et al., 2009). It is possible that the morphology has changed in response to the social system, rather than to the environment directly. This is a pattern seen in the hamadryas baboon, where males herd and directed aggression toward straying females, rather than towards other males, relaxing pressure for large male body size (Jolly and Phillips-Conroy, 2003). Prognathism may be related to canine size for display and agonistic encounters (Leutenegger and Cheverud, 1982, Plavcan et al., 1995).

In DFA, including both allometric shape and size controlled shape, olive baboons are only rarely misclassified into chacma, and no chacmas are misclassified as olive baboons. This demonstrates that the skulls are quite distinct. In contrast adjacent taxa tend to be misclassified more, such as the olive and yellow and hamadryas and olive baboon. One possibility is that the distinctiveness is eroded by the mistaken inclusion of hybrids, or else inclusion of specimens with a past history of hybridisation. If included, the influence of hybrids is likely to be small relative to the total sample. While gene flow and hybridisation do occur the extent to which this has opposed divergence over time is unknown. Nevertheless, the pattern of skull shape differences between the two largest *Papio hamadryas* subspecies conforms to the north-south pattern shown in the size-controlled trend surface analysis, and is concordant with the results of Frost et al. (2003). The visualisation presented here of narrower bizygomatic breadths and more ventrally flexed rostra for southern forms relative to northern also matches the work of Frost et al. (2003). Like Frost et al. (2003) we interpret this as reflecting phylogenetic history, reinforced by the observation that patterns of genetic variation are largely oriented in this axis (Zinner et al., 2009), with baboons likely to have originated in southern Africa before radiating north (Newman et al. 2004). The complexity and high genetic integration of the skull means that moving up and down the existing size-shape trajectory requires less genetic change than deviation from it (Marroig and Cheverud, 2005, Elton et al., 2010). Differences after

controlling for size indicate a divergent scaling trend between chacma and olive baboons and thus suggest a relatively deep phylogenetic split. This could be the result of a vicariance event or events during the Pleistocene allowing the accrual of genetic differences over time. Pleistocene environment fluctuations resulted in periods of increasing and decreasing aridification, potentially with periodic barriers to gene flux (Zinner et al., 2009). While these barriers are now relaxed, they may have profoundly altered baboon genetic structure (Zinner et al., 2009) and hence phenotype (Jolly and Phillips-Conroy, 2003, Charpentier et al., 2008). A similar explanation has been given for biological diversity in several polytypic African mammals (Hewitt, 2004), such as the eland (Lorenzen et al., 2010) and giraffe (Brown et al., 2007).

The differences between chacma and olive baboons illustrate the complexity of the processes that contributed to the skull morphology of modern *Papio hamadryas*. Phylogenetic differences may reflect adaptive signals relating to past environmental conditions. Also genetic isolation is likely to favour drift, and so morphological variation may be stochastic. Both these factors may play a part in determining baboon skull form. Adjacent populations typically show affinities (Jolly, 1993), and hence clinal variation, but there are discontinuities in certain traits relating to growth and form. Hamadryas baboons cease growing at an earlier stage than olive baboons (Jolly and Phillips-Conroy, 2003) and the olive baboon matures faster than the yellow baboon, ontogenetic features that are under strict genetic control rather than being the result of phenotypic plasticity (Charpentier et al., 2008). The chacma baboon also has a later peak testosterone level than the yellow baboon, again not the result of plasticity (Beehner et al., 2009). While these features are potentially ecologically adaptive, these genetic features are evidently canalised and not plastic. The distribution of these less labile genetic features is likely to be related to population history (or "zygostructure" Jolly, 1993). Added to these deeper rooted and heavily genetically determined examples of variation, proximate differences in, for example, resource availability or temperature, as discussed above, may lead to rapid alterations in size, which in turn can influence shape through allometry, and ultimately adaptation and population divergence (Elton et al. 2010).

To conclude, this study has found no evidence of a Bergmannian trend and no overarching relationship between baboon skull morphological variation and environmental variation. This suggests that, while important, thermoregulation is one of a variety of factors that contribute to morphological variation. Past rather than current environmental variation seems likely to have been the major driver of baboon morphological variation as a whole, by creating barriers to gene flow resulting in the highly spatial pattern of morphological variation described. Shallower subspecific

divisions manifest themselves as differences more related to allometric scaling, than deeper temporal division (and spatial distances). Subspecific morphological responses to environmental variation, potentially not related to environment directly but via the sociological factors cannot be ruled out.

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Authors' Contributions

Jason Dunn: carried out the analyses and wrote the paper.

Andrea Cardini: devised and supervised the analyses, collected the raw data and co-devised the concept.

Sarah Elton: supervised the research and the writing of the paper, and co-devised the concept.

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Table 1. The morphological sample broken down by subspecies and sex. The common names are as follows: *P. h. anubis* = olive, *P. h. cynocephalus* = yellow, *P. h. hamadryas* = hamadryas, *P. h. kindae* = Kinda, *P. h. papio* = Guinea, *P. h. ursinus* = chacma.

Subspecies	Sex	N
P. h. anubis	Male	120
	Female	56
P. h. cynocephalus	Male	63
	Female	11
P. h. hamadryas	Male	17
	Female	4
P. h. kindae	Male	11
	Female	11
P. h. papio	Male	13
	Female	1
P. h. ursinus	Male	45
	Female	9
		361

Table 2. Descriptions of the anatomical landmarks that were digitised to capture the three dimensional shape of the specimens (see Cardini et al., 2007).

No	Description
1	Prosthion: antero-inferior point on projection of pre-maxilla between central incisors
2	Prosthion2: antero-inferior-most point on pre-maxilla, equivalent to prosthion but between central and lateral incisors
3	Posterior-most point of lateral incisor alveolus
4	Anterior-most point of canine alveolus
5	Mesial P3: most mesial point on P3 alveolus, projected onto alveolar margin
6-9	Contact points between adjacent pre-molars/molars, projected labially onto alveolar margin
10	Posterior midpoint onto alveolar margin of M3
11-14	Contact points between adjacent pre-molars/molars, projected lingually onto alveolar margin
15	Posterior-most point of incisive foramen
16	Meeting point of maxilla and palatine along midline
17	Greater palatine foramen
18	Point of maximum curvature on the posterior edge of the palatine
19	Tip of posterior nasal spine
20	Meeting point between the basisphenoid and basioccipital along midline
21	Meeting point between the basisphenoid, basioccipital and petrous part of temporal bone
22	Most medial point on the petrous part of temporal bone
23	Most medial point of the foramen lacerum
24	Meeting point of petrous part of temporal bone, alisphenoid and base of zygomatic process of temporal bone
25-26	Anterior and posterior tip of the external auditory meatus
27	Stylomastoid foramen
28,30	Distal and medial extremities of jugular foramen
29	Carotid foramen
31	Basion: anterior-most point of foramen magnum
32,35	Anterior and posterior extremities of occipital condyle along margin of foramen

	magnum
33	Hypoglossal canal
34	Centre of condylar fossa
36	Opisthion: posterior-most point of foramen magnum
37	Inion: most posterior point of the cranium
38	Most lateral meeting point of mastoid part of temporal bone and supraoccipital
39	Nasospinale: inferior-most midline point of piriform aperture
40	Point corresponding to largest width of piriform aperture
41	Meeting point of nasal and pre-maxilla on margin of piriform aperture
42	Rhinion: most anterior midline point on nasals
43	Nasion: midline point on fronto-nasal suture
44	Glabella: most forward projecting midline point of frontals at the level of the supraorbital ridges
45	Supraorbital notch
46	Frontomalare orbitale: where frontozygomatic suture crosses inner orbital rim
47	Zygo-max superior: antero-superior point of zygomaticomaxillary suture taken at orbit rim
48	Centre of nasolacrimal foramen (fossa for lacrimal duct)
49	Centre of optic foramen
50	Uppermost posterior point of maxilla (visible through pterygomaxillary fissure)
51	Frontomalare temporale: where frontozygomatic suture crosses lateral edge of zygoma
52	Maximum curvature of anterior upper margin of zygomatic arch
53	Zygo-max inferior: antero-inferior point of zygomaticomaxillary suture
54	Zygo-temp superior: superior point of zygomaticotemporal suture on lateral face of zygomatic arch
55	Zygo-temp inferior: infero-lateral point of zygomaticotemporal suture on lateral face of zygomatic arch
56	Posterior-most point on curvature of anterior margin of zygomatic process of temporal bone
57	Articular tubercule
58	Distal-most point on post-glenoid process
59	Posterior-most point of zygomatic process of temporal bone
60	Foramen ovale (posterior inferior margin of pterygoid plate)
61	Meeting point of zygomatic arch and alisphenoid on superior margin of

	pterygomaxillary fissure
62	Meeting point of zygomatic arch, alisphenoid and frontal bone
63	Bregma: junction of coronal and sagittal sutures
64	Lambda: junction of sagittal and lamboid sutures
65	Antero-superior point of mandible between central incisors
66	Antero-superior point of mandible between lateral incisors
67	Posterior-most point of lateral incisor alveolus
68	Anterior-most point of canine alveolus
69	Mesial P3: most mesial point on P3 alveolus, projected onto alveolar margin
70-73	Contact points between adjacent pre-molars/molars, projected labially onto alveolar margin
74	Posterior midpoint onto alveolar margin of M3
75-78	Contact points between adjacent pre-molars/molars, projected lingually onto alveolar margin
79	Superior tip of coronoid process
80-81	Most lateral and most medial points on mandible condylar surfaces
82	Anterior-most point on roughening for attachment of masseter on inferior margin of the angle of mandible
83	Mandibular foramen
84	Posterior-most point on superior area of insertion of medial pterygoid
85	Region of insertion of genioglossus muscles (midline posterior-most point on upper ‘ridge behind incisors’)
86	Region of insertion of geniohyoid muscles (midline posterior-most point on lower ‘ridge behind incisors’)

Table 3. Exploratory investigation of correlations between gsPCs and centroid size.

Sample size	Geospatial PC	Pearson Correlation
112	1	-0.310
	2	-0.338
	3	-0.106
106	1	-0.455
	2	-0.566
	3	-0.102

Table 4. Discriminant analyses showing the percentage cross validated classification rates for the six subspecies for shape and size controlled shape.

Shape	Subspecies	Predicted Group Membership					
		P. h. papio	*P. h. hamadryas*	*P. h. Anubis*	*P. h. cynocephalus*	*P. h. ursinus*	*P. h. kindae*
Actual	*P. h. papio*	100.00	0.00	0.00	0.00	0.00	0.00
	P. h. hamadryas	0.00	77.78	11.11	11.11	0.00	0.00
	P. h. Anubis	2.04	4.08	75.51	12.24	6.12	0.00
	P. h. cynocephalus	0.00	0.00	25.00	65.00	10.00	0.00
	P. h. ursinus	0.00	0.00	0.00	12.00	88.00	0.00
	P. h. kindae	0.00	0.00	0.00	0.00	0.00	100.00
Size controlled	*P. h. papio*	100.00	0.00	0.00	0.00	0.00	0.00
	P. h. hamadryas	0.00	44.44	55.56	0.00	0.00	0.00
	P. h. anubis	4.08	4.08	75.51	14.29	2.04	0.00
	P. h. cynocephalus	0.00	0.00	35.00	55.00	10.00	0.00
	P. h. ursinus	0.00	0.00	0.00	4.00	68.00	28.00
	P. h. kindae	0.00	0.00	0.00	0.00	66.67	33.33

Table 5. The results of the partial regression, displaying the percent of variance explained by four components: the exclusive spatial and environmental component, their common overlap and the residual. Values are displayed for all models and the holdouts.

Model		Spatial (%)	Common (%)	Environmental (%)	Residual (%)
All subspecies	Shape (full)	20.8	1.8	5.5	71.9
	Shape holdout 1	23.8	0.0	7.0	69.2
	Shape holdout 2	20.1	2.9	8.2	68.8
	Shape holdout 3	21.6	4.5	8.5	65.4
Kinda baboon excluded	Shape (full)	27.5	1.7	6.6	64.2
	Shape holdout 1	30.3	0.6	9.3	59.9
	Shape holdout 2	25.8	4.4	9.3	60.5
	Shape holdout 3	29.3	4.6	8.6	57.5
All subspecies	Size (full)	23.0	1.7	6.6	68.8
	Size holdout 1	25.0	1.6	7.0	66.4
	Size holdout 2	23.1	-3.0	11.3	68.6
	Size holdout 3	21.1	5.9	11.3	61.7
Kinda baboon excluded	Size (full)	51.1	4.7	2.7	41.5
	Size holdout 1	52.5	8.5	1.3	37.7
	Size holdout 2	42.9	3.1	8.0	46.0
	Size holdout 3	58.0	8.6	4.5	28.9
All subspecies, size controlled	Shape (full)	22.1	0.4	7.9	69.6
	Shape holdout 1	24.6	0.0	10.9	64.5
	Shape holdout 2	24.8	2.0	9.8	63.4
	Shape holdout 3	23.7	0.7	10.8	64.8

Table 6. Results of regressions of centroid size on environmental terms for different subspecies. Temp. M. = mean temperature, Temp. SD = standard deviation of monthly temperature, Prec. M. = mean precipitation in mm, Prec. SD = standard deviation of monthly rainfall, Most. M. = mean moisture index, Moist. SD = standard deviation of monthly moisture index, Shan. Div. = Shannon diversity index of monthly rainfall. A conservative Bonferroni correction for multiple tests was used ($\alpha = 0.006$).

Model	n	NDVI		Altitude		Temp. M.		Temp SD	
		F	P	F	P	F	P	F	P
All subspecies	*112*	2.145	0.099	0.942	0.334	0.801	0.373	1.935	0.167
All subspecies minus *P. h. kindae*	*106*	1.313	0.274	3.755	0.055	0.344	0.559	0.402	0.527
P. h. Anubis	*48*	0.206	0.652	1.559	0.218	6.067	0.017	0.258	0.614
P. h. cynocephalus	*19*	0.503	0.487	0.503	0.487	5.061	0.037	0.331	0.572
P. h. hamadryas	*7*	0.028	0.871	1.594	0.247	0.088	0.776	0.069	0.801
P. h. kindae	*5*	1.040	0.365	0.415	0.554	0.084	0.787	1.823	0.248
P. h. papio	*2*	0.093	0.812	2.954	0.335	59.911	0.082	2.693	0.348
P. h. ursinus	*24*	0.691	0.414	1.361	0.255	3.214	0.086	2.879	0.103

Table 6. Continued.

Model	n	Prec. M.		Prec. SD		Moist. M.		Moist. SD		Shan. Div.	
		F	P	F	P	F	P	F	P	F	P
All subspecies	*112*	0.040	0.841	0.538	0.465	0.233	0.630	0.132	0.717	0.382	0.538
All subspecies minus *P. h. kindae*	*106*	1.538	0.218	2.625	0.108	0.002	0.964	0.342	0.560	0.205	0.652
P. h. Anubis	*48*	3.412	0.071	12.727	**0.001**	0.026	0.871	6.118	0.017	0.942	0.337
P. h. cynocephalus	*19*	0.316	0.581	1.041	0.321	0.020	0.888	0.751	0.398	0.137	0.716
P. h. hamadryas	*7*	0.020	0.892	0.022	0.886	0.008	0.933	0.000	0.984	0.310	0.595
P. h. kindae	*5*	0.167	0.704	0.073	0.800	1.348	0.310	0.097	0.771	1.899	0.240
P. h. papio	*2*	0.005	0.955	0.389	0.645	0.040	0.875	13.679	0.168	0.017	0.917
P. h. ursinus	*24*	1.084	0.309	0.382	0.543	3.823	0.063	0.089	0.768	1.696	0.206

FIGURE LEGENDS

Figure 1. The geographic ranges of the six baboon subspecies (IUCN, 2011) and a phylogenetic schematic (based on mt haplogroups of Zinner et al., 2011). Please note that the distribution illustrated here represents the one used by the authors in analysis but that the exact transition points from *P. h. kindae* to *P. h. cynocephalus* and *P. h. ursinus* are debated due to the complex nature of phenotypic and genotypic variation, resulting from hybridisation at range edges, in the Kinda baboon.

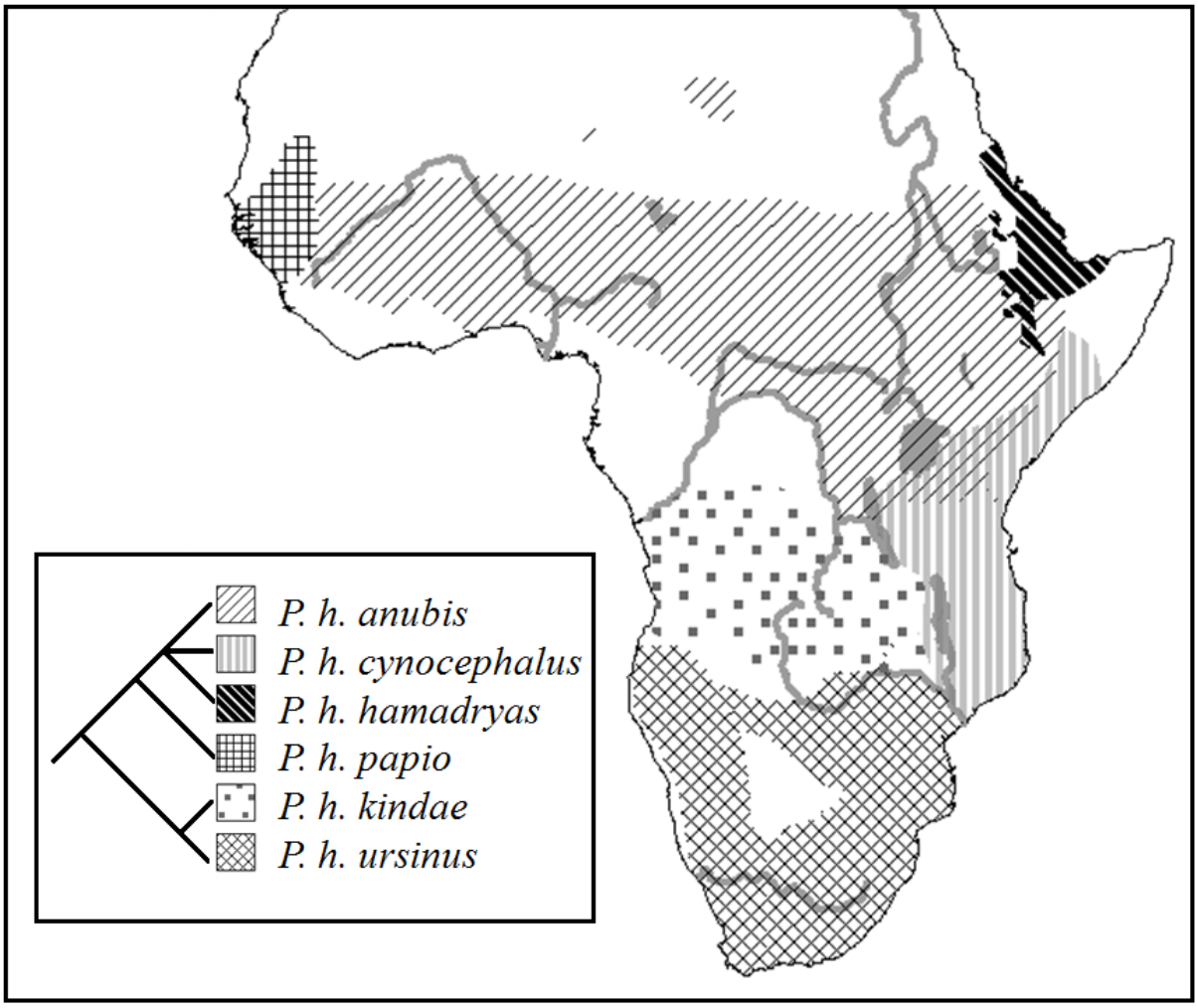

Figure 2. The location of baboon specimens for all taxa (n=112), where point size is proportional to the centroid size of the skull.

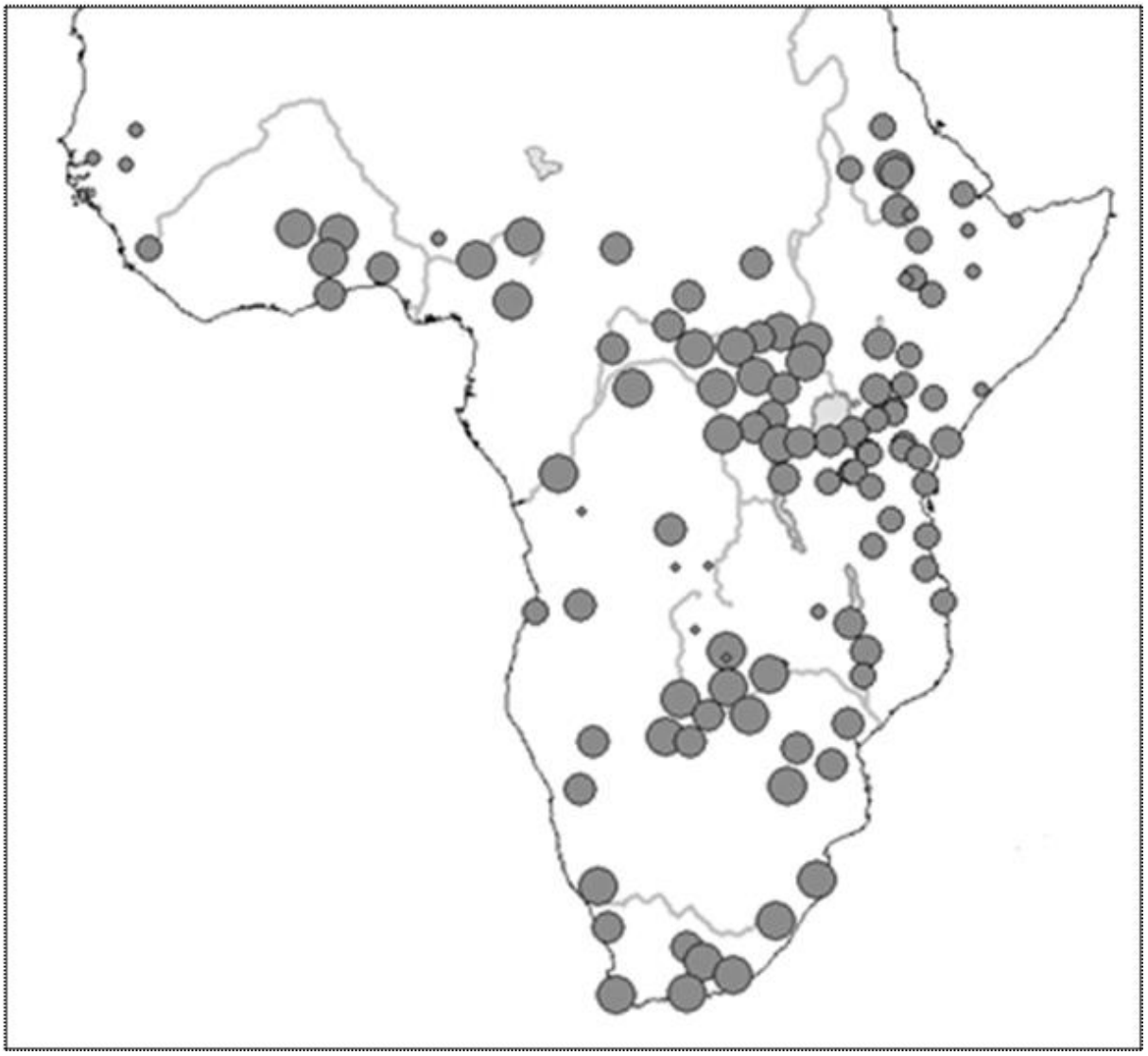

Figure 3. The baboon size trend surface analysis for **a)** all taxa minus *P. h. kindae* and **b-d)** the three holdouts. Terms in regression **a)** were x y^2 x^3 xy^2, variance explained 55.9%. n =106. The holdout trends explained **b)** 33.0, **c)** 72.3 and **d)** 22.4% of the variance of the randomly omitted third. Point size is proportional to the modelled centroid size of the skull

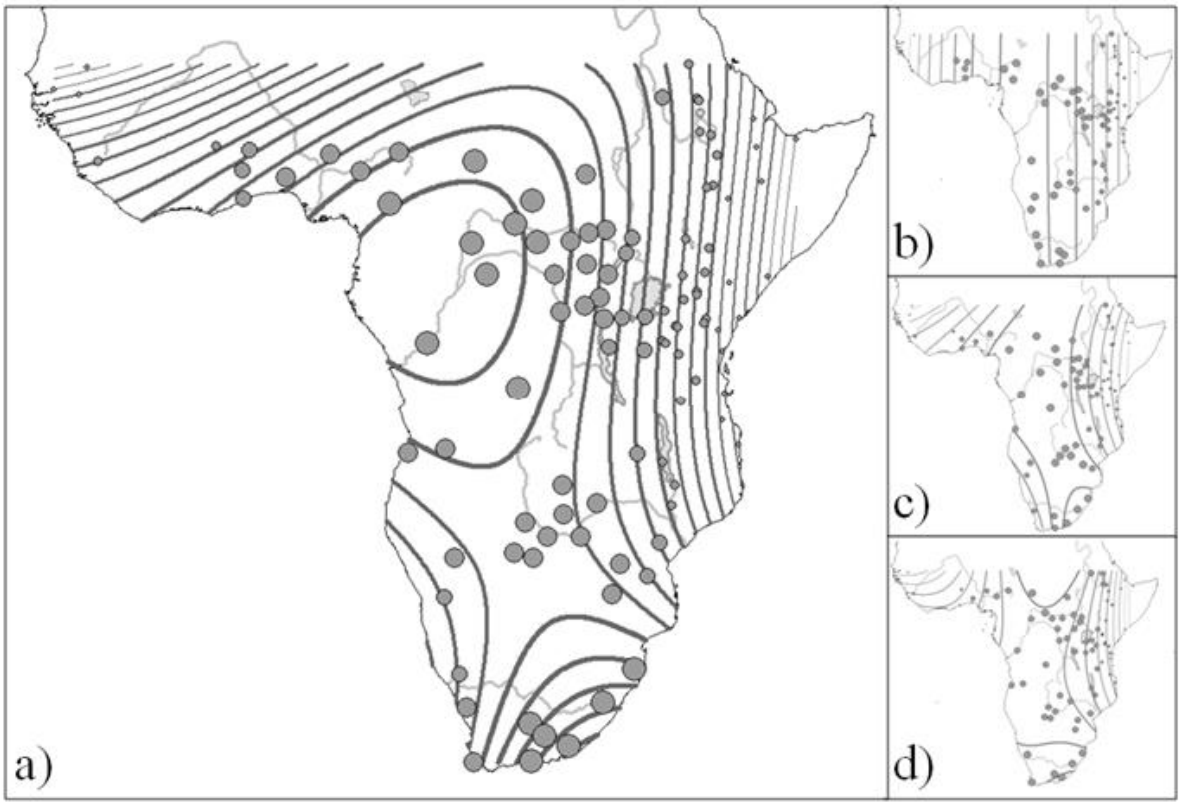

Figure 4. The baboon size trend surface analysis for a) all baboon taxa b-d) the three holdouts. Terms in regression **a)** were xy x^3 x^2y y^3, variance explained 24.7%, n =106. The holdout trends explained **b)** 9.7, **c)** 29.5 and **d)** 18.2% of the variance of the randomly omitted third. Point size is proportional to the modelled centroid size of the skull

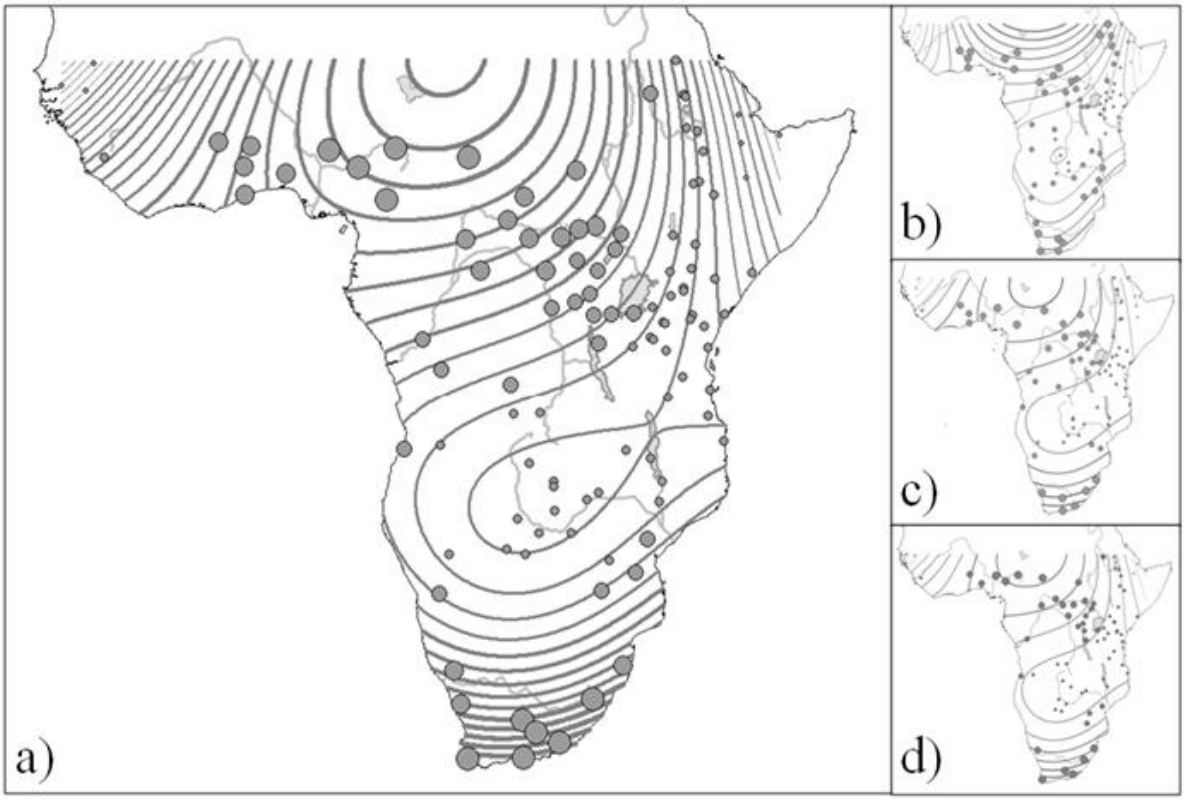

Figure 5. The first three gsPCs for baboon shape without *P. h. kindae* (n = 106). Variance explained by **a)** gsPC1 = 57.3%, **b)** gsPC2 = 16.3%, and **c)** gsPC3 = 9.0%. Visualisations are exaggerated by a factor of 2.5 to aid interpretation. Point size is proportional to the gsPC score of the skull.

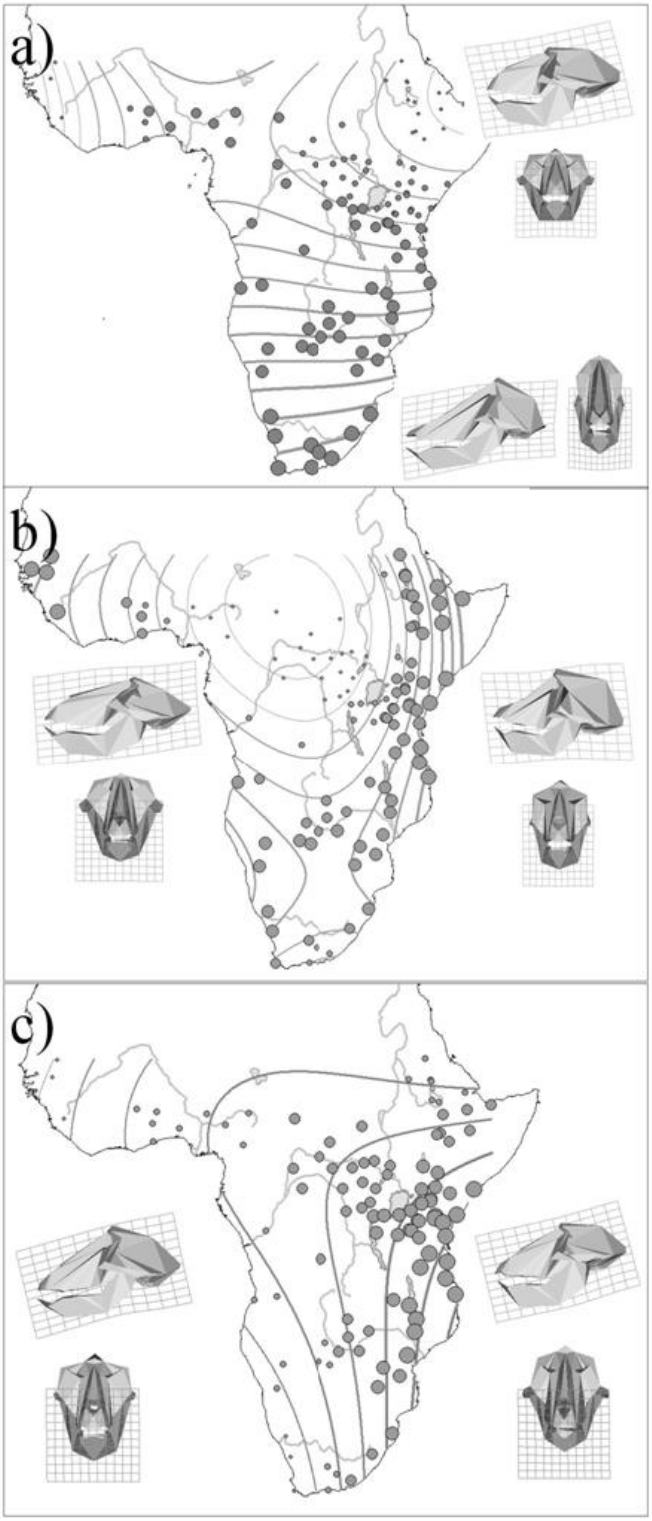

Figure 6. The first three gsPC for baboon shape including *P. h. kindae* (n = 112). Variance explained by **a)** gsPC1 = 57.3%, **b)** gsPC2 = 16.3%, and **c)** gsPC3 = 9.0%. Visualisations are exaggerated by a factor of 2.5 to aid interpretation. Point size is proportional to the gsPC score of the skull.

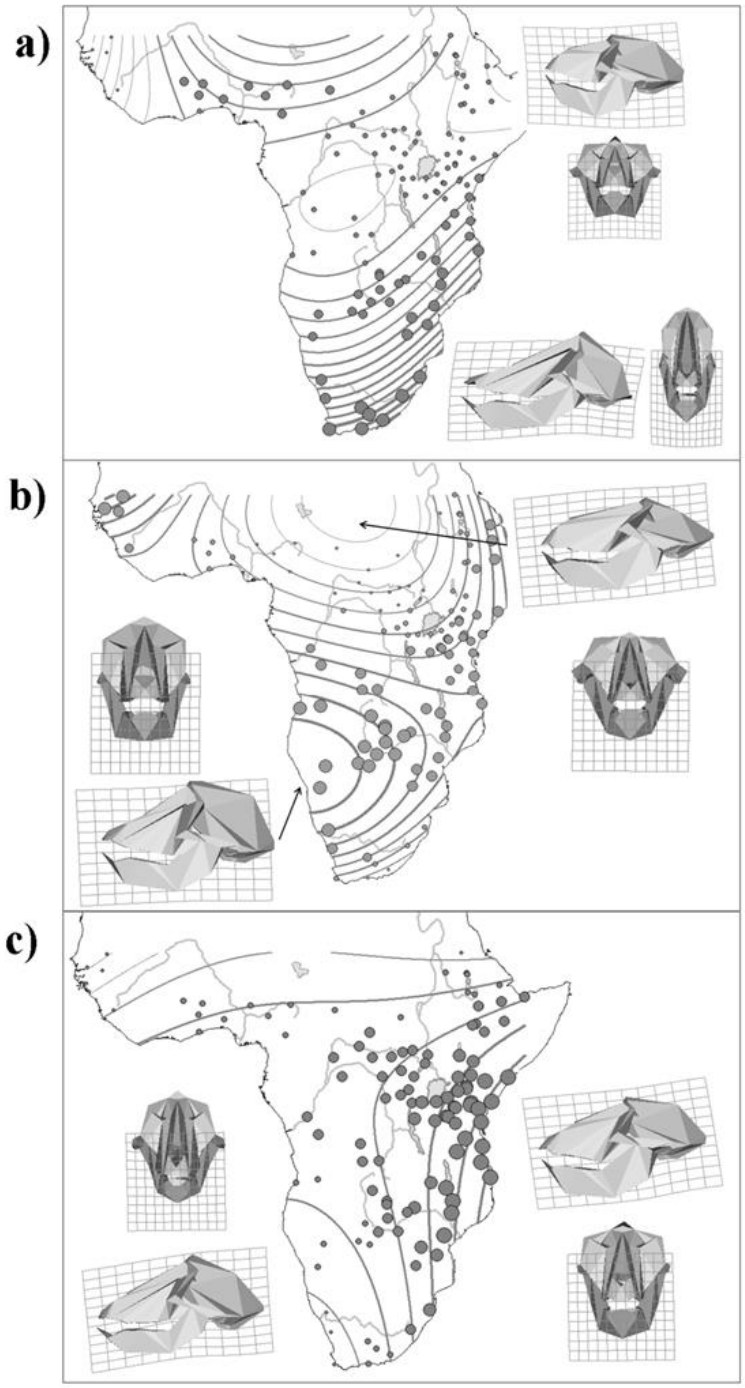

Figure 7. Size-controlled geospatial PCs for the full dataset (n=112). Percentage of variance explained by **a)** SCgsPC1 is 61.0% **b)** SCgsPC2 is 14.5% **c)** SCgsPC3 is 8.7%. Visualisations exaggerated by a factor of 2.5 to aid interpretation. Point size is proportional to the gsPC score of the skull.

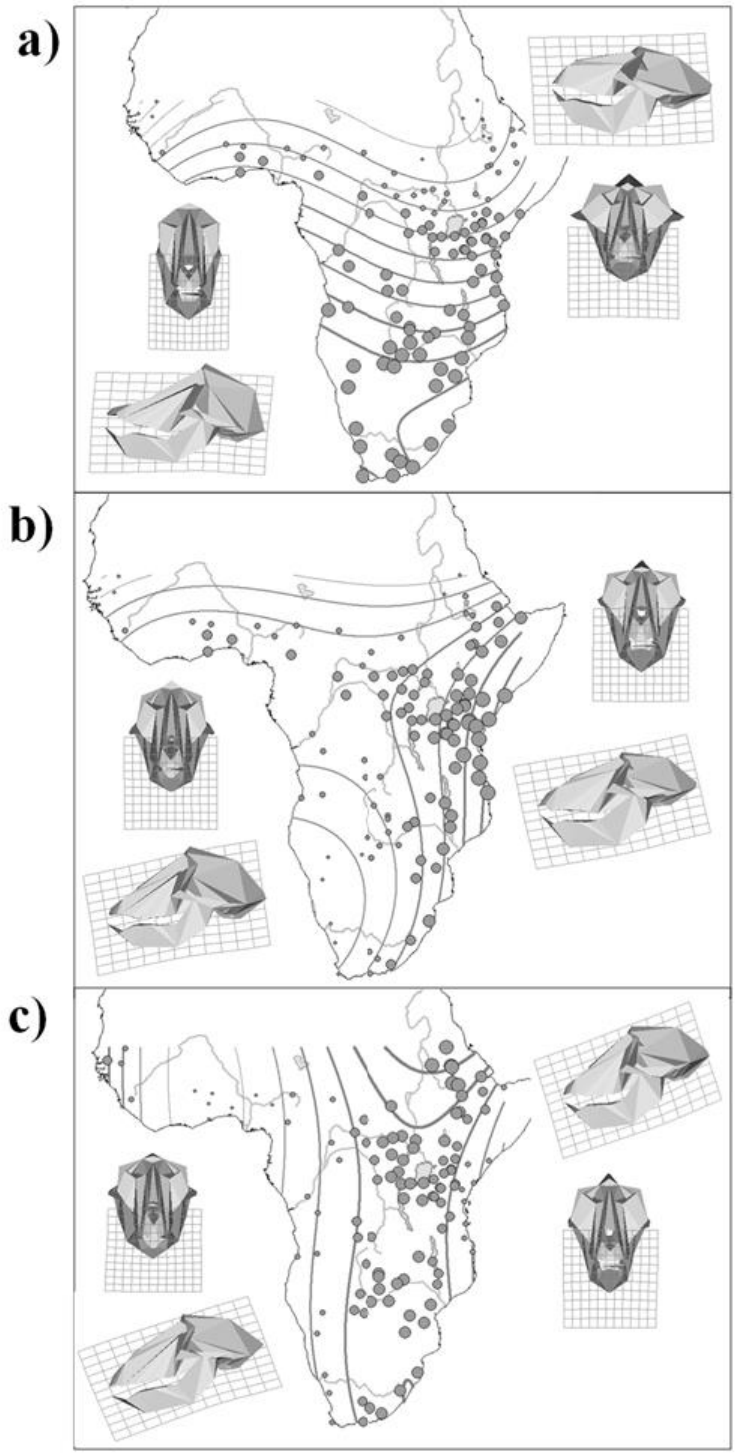

Figure 8. Partial Regression results showing the percentages of variance explained by significant spatial terms, environmental terms (precipitation, moisture index, temperature, NDVI, altitude, P2T, seasonality index, Shannon Rainfall index) and their overlap for size, shape, size controlled shape and all the holdout with and without the Kinda baboon sample.

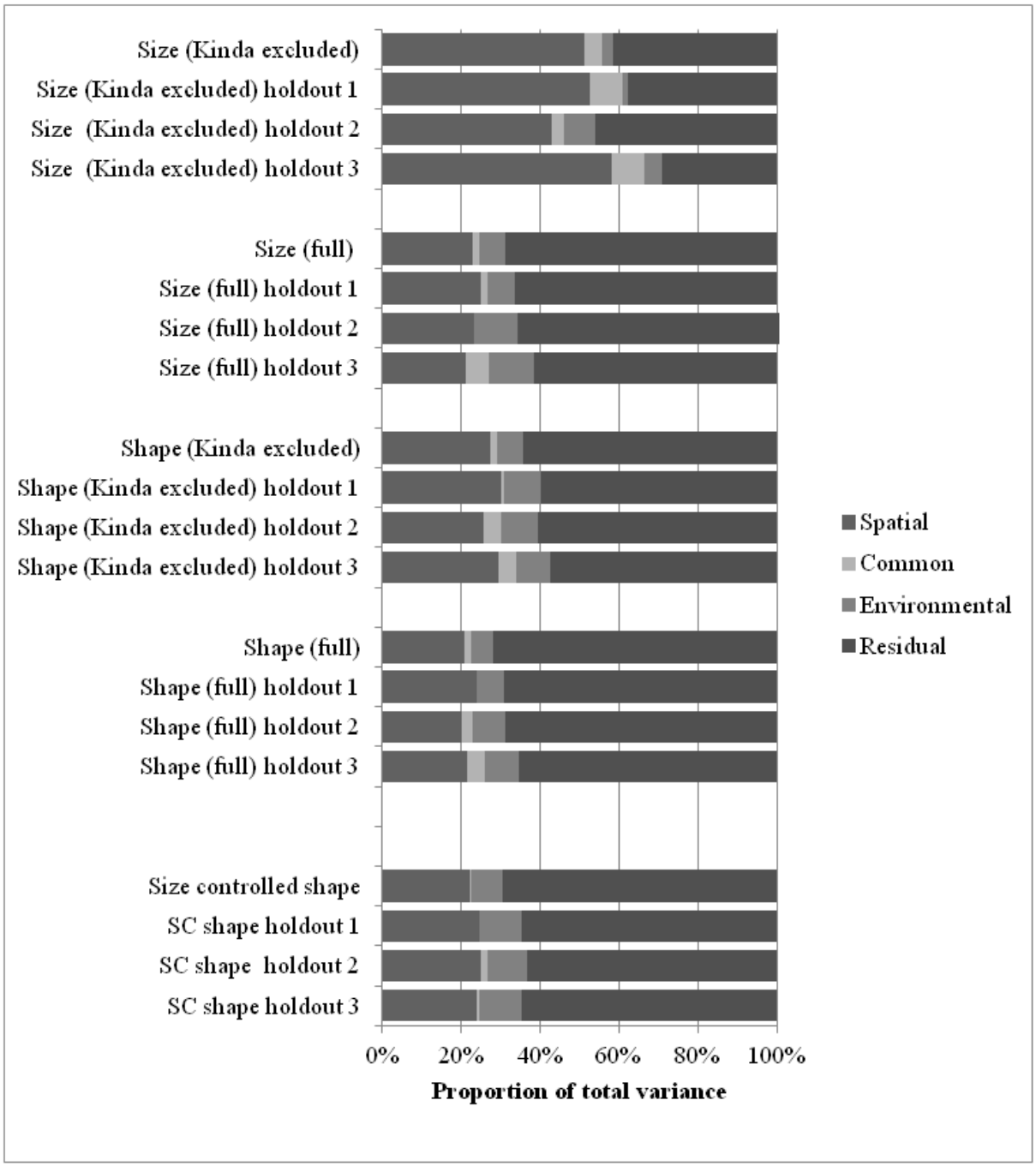

Figure 9. Showing *P. h. anubis* centroid size against standard deviation of precipitation (R^2 = 0.213).